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Research Article

# Eco-evolutionary experience outweighs soil effects in shaping *Senecio inaequidens* invasion success

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## Abstract

Introduced species encounter novel biotic and abiotic conditions that influence their success in new environments. Their advantages often arise from reduced competition with species lacking eco-evolutionary experience and from their capacity to preempt or efficiently use resources. Once established, their success can also be shaped by interactions with soil microbial communities. Understanding how these factors influence invasion success can provide valuable insights into identifying the mechanisms that enable certain species to become dominant in a plant community. In this study, we examined how eco-evolutionary experience and invaded-range soil bacterial communities modulate the performance of the invasive subshrub *Senecio inaequidens* DC. We conducted a fully factorial additive experiment in growth chambers, with *S. inaequidens* individuals growing at the center of each pot. The design included two factors: (1) competitor community identity with three levels (i.e., plant species from the native range (South Africa), species from the invaded range (Italy), and a control with no competitor species); and (2) soil biotic conditions with two levels (i.e., autoclaved soil with reduced microbial load and non-autoclaved soil). Our results showed that plant community identity had the strongest effect on *S. inaequidens* growth (height and lateral spread), with the smallest individuals occurring in competition with species from the native range. Growing on autoclaved soil had no major impact on plant height, suggesting that soil microbial communities played a minor role modulating competitive interactions, which were the dominant driver of plant growth responses. Suppression was strongest when competitors were phylogenetically closer to *S. inaequidens*, especially those from its native range. Soil bacterial communities were influenced by both competitor community identity and soil treatment, with lower bacterial diversity found in pots with better *Senecio* plant growth. These results indicate that promoting competition with closely related natives and maintaining diverse soil microbiota may limit invasion success.

**Key words:** Eco-evolutionary experience, phylogenetic similarity, plant traits, relatedness, soil bacteria, South African ragwort

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## Introduction

Upon entering new environments, introduced species encounter novel biotic and abiotic conditions that can either facilitate or hinder their establishment (Heger et al. 2019). To become successful invaders, these species must not only establish in an area but also develop effective interactions within the recipient community and efficiently utilize and compete for available resources (Funk and Vitousek 2007). In doing so, introduced plants may encounter not only new competitors but also pathogens, herbivores, or other antagonistic organisms (Funk et al. 2008), lose critical mutualistic interactions (Mitchell et al. 2006), or face novel traits such as allelochemical release, with which they lack eco-evolutionary experience (Cummings et al. 2012; Yuan et al. 2021). The outcome of these novel interactions is largely determined by the eco-evolutionary history of both introduced and native species (Saul et al. 2013; Saul and Jeschke 2015). Such eco-evolutionary experience may arise from long-term evolutionary processes or from more recent ecological interactions. In other words, species that have previously encountered similar traits, enemies, or mutualists in the native range are therefore better adapted to successfully establish in new assemblages where such interactions are present (Saul et al. 2013). In contrast, resident naïve communities may show weaker adaptive responses, influencing invasion outcomes when faced with species containing new interactions with introduced species (Heger and Trepl 2003; Heger et al. 2019). Understanding these mechanisms provides valuable insight into why some species become dominant and how processes such as range expansion and future invasions may unfold under global change (Fristoe et al. 2021).

Competition for limited resources arising from niche overlap is a key determinant of the success of introduced plant species at the community level. Because closely related species often share traits shaped by similar eco-evolutionary interactions, phylogenetic distance can serve as a proxy for predicting competitive outcomes and thus the ability of an introduced species to tolerate suppression by competing species in the recipient community ("competitive response," Goldberg 1990; MacDougall et al. 2009). In this context, Darwin's naturalization hypothesis posits that introduced species are less likely to establish in communities dominated by closely related natives but more likely to succeed when they are phylogenetically distant from resident species (Darwin 1859; Daehler 2001; Yannelli et al. 2025). This assumption rests on the idea that niche similarity is phylogenetically conserved (Prinzing 2001), with relatedness reflecting shared traits that shape coexistence potential (Blomberg and Garland 2002). Conversely, phylogenetically distant invaders may gain a competitive advantage by possessing novel traits or by escaping natural enemies in the recipient community that lacks a coevolved history with the newcomer (Fan et al. 2023). Although this hypothesis has been instrumental in explaining early stages of invasion (Park and Potter 2013; Yannelli et al. 2017), inconsistencies arise from temporal variation and shifts in traits among closely related species (Burns and Winn 2006; Thuiller et al. 2010; Li et al. 2015). Furthermore, the hypothesis has rarely been tested with species from both native and invaded ranges (Zheng et al. 2018).

Novel associations with antagonistic or mutualistic microorganisms may emerge in the invaded range based on functional trait similarities with local species, even without a shared evolutionary history (Eppinga et al. 2006; Diez et al. 2010). These associations with microorganisms, which can arise either through the loss

of interactions maintained in the native range or through the formation of novel interactions in the invaded range, can mediate competitive, mutualistic, and antagonistic interactions between introduced and competitor plant species in the recipient community (Abbott et al. 2015; Fahey and Flory 2022). For instance, introduced plants may gain a competitive advantage by escaping coevolved specialist pathogens from their native range (Mitchell and Power 2003; Fahey and Flory 2022) or by serving as reservoirs for pathogens that disproportionately affect native species (Eppinga et al. 2006; Mangla and Callaway 2008).

Following successful establishment, trait differences between introduced plants and those in recipient communities, particularly those associated with acquisitive strategies, may lead to shifts in the microbial community from fungi-dominated to bacteria-dominated systems (Ehrenfeld 2003; Wardle et al. 2004; Torres et al. 2021). Such shifts can alter the diversity and structure of the entire microbial community. In some cases, introduced species may select for or promote specific bacterial strains that modify soil conditions to their benefit, further enhancing their invasion success (Kourtev et al. 2002; Callaway et al. 2004; Zhang et al. 2023). Despite growing evidence for these soil-mediated mechanisms, our knowledge of the role of soil bacteria in mediating competition and how introduced plants influence these communities remains highly limited (van der Putten et al. 2007; Dawson and Schrama 2016).

To understand the role of eco-evolutionary experience and soil-mediated feedbacks in shaping competitive success across native and invaded ranges, we selected the invasive plant *Senecio inaequidens* DC., commonly known as "South African Ragwort" or "Canary Weed," as our study species (hereafter sometimes referred to by its generic name). This perennial chamaephyte, native to Southern Africa, was introduced to Europe in the late 19$^{th}$ century (Ernst 1998) and has since become invasive in disturbed areas, including regions of Southern Africa outside its native range. *Senecio inaequidens* has been found to produce allelopathic defenses in the form of pyrrolizidine alkaloids (Scherber et al. 2003), which can deter above- and belowground herbivores (Caño et al. 2009; Thoden et al. 2009) and influence soil microbial communities (Harkes et al. 2017). Its functional traits have also been linked to rhizosphere composition, with bacterial diversity being positively correlated with greater resource allocation to root growth and late flowering (Thébault et al. 2010). Moreover, *S. inaequidens* can alter soil abiotic conditions by enriching nutrient concentrations through litter inputs, which may facilitate the growth of co-occurring native species in nutrient-poor environments (Van De Walle et al. 2022; Quaglini et al. 2025b).

In this study, we therefore investigated the competitive response of *S. inaequidens* to plant species from both its native and invaded ranges under controlled conditions, as well as the role that soil microbial communities from the invaded range have in modulating this response. The experimental communities comprised species with which *S. inaequidens* shares a history of eco-evolutionary interactions (native range) and species to which it is evolutionarily naïve (invaded range). We then evaluated whether eco-evolutionary experience, phylogenetic distance among the plant species, and soil biotic conditions better explained *S. inaequidens* performance. We hypothesized that (i) *S. inaequidens* performance will depend on the identity of the competing communities and will be better when competing with evolutionarily naïve species from the invaded range than with experienced species from the native range; and that (ii) an increase in phylogenetic distance between

*S. inaequidens* and the competitor species in the community will result in higher performance of *S. inaequidens*, consistent with Darwin's naturalization hypothesis. We also explored how reducing soil biota from the invaded range through autoclaving influenced these competitive interactions and the effect that competitor communities and *S. inaequidens* had on soil bacterial diversity.

## Materials and methods

### Plant and soil material collection

*Senecio inaequidens* is a subshrub that belongs to the Asteraceae family, often reaching 40–100 cm in height. Native to the highlands of Southern Africa, it was introduced to Europe as a wool contaminant (Ernst 1998). It thrives in disturbed areas such as roadsides, railways, and quarries, as well as dry grasslands, pastures, and vineyards (Heger and Böhmer 2005; López-García and Maillet 2005). In its native range, the species exists in diploid (2n = 20) and tetraploid (2n = 40) forms, but only tetraploids are found in Europe (Lafuma et al. 2003).

Seeds of *S. inaequidens* were collected from a population located in the former quarry of Collepedrino, Northern Italy, which is currently heavily invaded by this species (Bergamo, 45°46'37.4"N, 9°31'09.5"E). To design the competing communities, we chose species known to co-occur with *S. inaequidens* in both the native and invaded ranges. To select those from the native range (i.e., South Africa), we used the National Collections database (formerly hosted at http://posa.sanbi.org/) to select species documented in the area where tetraploid populations of *S. inaequidens* have been reported (Lafuma et al. 2003). Based on availability in local seed companies and to ensure that all species would have co-occurred within a plot-sized area, we refined the list of species by a second check against the results of vegetation surveys (Du Preez and Bredenkamp 1991). As a result, we selected a multi-species suite comprising five species: *Aristida congesta* Roem. & Schult. (Poaceae), *Hibiscus trionum* L. (Malvaceae), *Salvia disermas* L. (Lamiaceae), *Wahlenbergia androsacea* A.DC., and *Wahlenbergia undulata* (L.f.) A.DC. (Campanulaceae) for the native range. None of the species from the native range occurred in the study area in the invaded range, although *Hibiscus trionum* is naturalized in some areas of Italy (https://www.cabidigitallibrary.org/doi/full/10.1079/cabicompendium.27133#REF-DDB-55157). Seed material for this range was purchased from the local seed company Silverhill (Cape Town, South Africa). In the invaded range (i.e., Italy), we selected native species according to known co-occurrence in the Collepedrino quarry (Gentili et al. 2020) and collected seeds in the same area. The list included five species: *Bromopsis erecta* (Huds.) Fourr. (Poaceae), *Hypericum perforatum* L. s.l. (Hypericaceae), *Onobrychis viciifolia* Scop. (Fabaceae), *Poterium sanguisorba* L. s.l. (Rosaceae), and *Trifolium repens* L. (Fabaceae). We performed germination tests for all species to determine the best conditions for their germination (Suppl. material 1: information S1, table S1).

Soil used for the experiment was collected in the same quarry. It was placed in open dry bags and stored at room temperature for about 1 month until the experiment was set up. We prepared the experimental substrate by mixing the quarry soil, which was highly rocky, with common potting substrate (TERCOM potting soil) in a 1:1 ratio to favor plant growth under controlled conditions (growth chamber). Before setting up the pot experiment, we autoclaved half of this soil mix at 120 °C for 45 min.

## Experimental design and setting

Our experiment consisted of a fully factorial design combining two factors: competitor community identity and soil biotic conditions (Suppl. material 1: fig. S1). The competitor community identity had three levels, namely species from the native range (SA; South Africa), species from the invaded range (IT; Italy), and the control (CTR; Control), with *S. inaequidens* individuals growing alone. Soil biotic conditions had two levels, i.e., autoclaved and non-autoclaved soil. Each treatment combination was replicated five times, resulting in a total of 30 experimental pots.

All seeds used were stratified by placing them in paper bags at 4 °C for about 1 month. Two different germination methods were used to ensure seed survival and high germination rates. These were determined according to the results of germination tests performed before the experiment and consisted of (1) germinating seeds directly in plastic cups with a mix of autoclaved common potting soil and sand at a 1:1 ratio and (2) germinating seeds in Petri dishes with moistened filter paper, followed by transplantation to plastic cups filled with autoclaved common potting soil and sand at a 1:1 ratio; a few days after germination (see protocols in Suppl. material 1: information S1). When seedlings were about 20 days old, we placed two individuals of *S. inaequidens* in the middle of 2 L pots filled with a mix of quarry soil and common potting soil in all pots. At the same time, in all treatment combinations with competition, we added five individuals of each competitor species distributed at the edges of the pot (for a total of 27 individuals in community competition pots, 25 competitor individuals and two *S. inaequidens* plants). Control treatments had no competitor species added, only the *S. inaequidens* plants. We then completely randomized the pots and placed them in a growth chamber with an average temperature of 29 °C, relative humidity of 42%, and a day–night cycle of 14 and 10 hours, respectively. These values were consistent with the growth conditions of *S. inaequidens* when invading ruderal dry habitats (railways, roadsides, and others). Plants were watered every other day for the first 15 days and twice a week for the remainder of the experiment (approximately 27 watering events in total). Pots were monitored for mortality to ensure sufficient replicates for analyses.

## Measurements and data processing

At 84 days, because of the mortality of some *S. inaequidens* individuals, we considered the competition experiment concluded. We recorded plant vegetative fitness, as a proxy for success, by measuring the maximum height and lateral growth of the surviving *S. inaequidens* individuals. Plant height was measured as the shortest distance between the upper boundary of the main photosynthetic tissues of a plant and ground level, which is known to be strongly correlated with aboveground biomass in herbaceous species (Pérez-Harguindeguy et al. 2013; Proulx 2021). The lateral growth of each individual of *S. inaequidens* was measured as the maximum width of the canopy (Pérez-Harguindeguy et al. 2013). When two individuals of *S. inaequidens* survived, we used the mean of the maximum height and width of the plants for further calculations. At this point, we also recorded the number and identity of the surviving species in the competitor community in each pot.

To assess the effect of relatedness on *S. inaequidens* performance, we calculated the phylogenetic distances among all species in our experiment using a phyloge-

netic tree for angiosperms as a backbone (Zanne et al. 2014). To do so, the tree was pruned by removing all species that were not included in our experiment (Suppl. material 1: fig. S2). We then calculated competitor community-weighted phylogenetic distances to *S. inaequidens* by weighting the community–*Senecio* distances by the proportion of each species in the competitor community in the pot. This proportion was calculated based on the total number of individuals alive of each species (not the survival rate). Further, we obtained the distance of the most abundant species in each community to *S. inaequidens* to examine the effect of these species on its growth. In the case of more than one species dominating the community, namely having the same number of individuals in the pot, we used the mean phylogenetic distance to all dominant species. We included both phylogenetic metrics because they capture complementary aspects of the competitors' influence: the weighted mean distance reflects the overall phylogenetic structure of the community, including rare species, whereas the distance to the most abundant species isolates the effect of dominant competitors. To characterize the soil bacterial communities in each treatment combination, we collected soil samples at the end of the experiment (after 84 days) from three randomly selected pots per treatment combination (n = 18). The samples were stored at –20 °C until processing.

## DNA extraction and next-generation sequencing

Genomic DNA was extracted using the FastDNA® Spin Kit for Soil (MP Biomedicals, Solon, OH, USA) following the manufacturer's instructions. A first PCR amplification was carried out using the 27F (5'-AGAGTTTGATCMTGGCTCAG-3') and 519R (5'-GWATTACCGCGGCKGCTG-3') primers (Frank et al. 2008) on the original DNA extract and on the 1:10, 1:100, 1:1000, and 1:10000 dilutions to detect the possible presence of PCR inhibitors. Amplification conditions were as follows: initial denaturation at 95 °C for 4 min; 29 cycles at 95 °C for 30 s, 55 °C for 45 s, and 72 °C for 45 s; and a final extension at 72 °C for 5 min. A second PCR was then performed using 783F and 1046R primers targeting the V5–V6 hypervariable regions of the bacterial 16S rRNA gene, with customized oligonucleotide barcodes (6 bp; see sequence in Table S2) added to their 5' end (Gandolfi et al. 2024). We used GoTaq® Green Master Mix (Promega Corporation, Madison, WI, USA) and 1 μM of each primer for a final volume of 2 × 50 μL for each sample. This second amplification was performed under the following conditions: initial denaturation at 94 °C for 4 min; 28 cycles at 94 °C for 50 s, 47 °C for 30 s, and 72 °C for 30 s; and a final extension at 72 °C for 5 min. The PCR products were purified using the Wizard® SV Gel and PCR Clean-Up System (Promega Corporation, Madison, WI, USA), following the manufacturer's instructions, and the DNA content was quantified with the Qubit® 2.0 fluorometer (Life Technologies, Carlsbad, CA, USA). Amplicon libraries were prepared with nine samples each, identifiable due to different barcode pairs. Library preparation, including the addition of standard Nextera indices (Illumina, Inc., San Diego, CA, USA), and sequencing with the MiSeq Illumina platform (Illumina, Inc., San Diego, CA, USA) using a 2 × 250 bp paired-end protocol, were performed at the Consorzio per il Centro di Biomedicina Molecolare (CBM), located in Trieste, Italy. Amplicon sequence variants (ASVs) were inferred through the DADA2 algorithm (Callahan et al. 2016), as described in Gandolfi et al. (2024).

## Data analysis

All statistical analyses were performed using R version 4.3.1 (R Core Team 2023) and the *vegan* package (Oksanen et al. 2022), unless stated otherwise. We used two-way ANOVA to assess whether the average height and lateral growth of *S. inaequidens* were influenced by the competitor community, invaded-range soil conditions, and their interaction. Because there was an imbalance in experimental replication due to the mortality of *S. inaequidens* in some replicates, we used the Type III test. We then performed post hoc pairwise comparisons using Tukey's tests. To evaluate whether phylogenetic relatedness influenced average *S. inaequidens* height and lateral growth, we used linear regressions. We first used community-weighted phylogenetic distance to *S. inaequidens*, or the phylogenetic distance of the most abundant species, together with soil biotic conditions, as explanatory variables, and then fitted a second set of models without differentiating soil biota effects. Prior to modeling, multicollinearity among explanatory variables was assessed using pairwise Pearson correlation coefficients, and no strong correlations were detected.

We used non-metric multidimensional scaling (NMDS) analysis based on Bray–Curtis dissimilarity distances (Bray and Curtis 1957) to visualize differences in soil bacterial community structure according to the treatments using the *metaMDS* function. The NMDS analysis had a stress coefficient below 0.2 in two dimensions (0.128), thus indicating that this number of dimensions provided a good representation of our data (Clarke 1993). We carried out a PERMANOVA test using the adonis2 function to assess the effects of treatment combinations on soil bacterial communities. Before performing these multivariate analyses, we transformed the bacterial ASV abundance matrix using the Hellinger distance to reduce the emphasis on ASV abundances while highlighting their presence or absence and mitigating the double-zero issue when comparing ASV compositions across samples (Borcard et al. 2018). We calculated ASV richness and the Shannon index for each treatment combination on the rarefied bacterial data, based on the sample with the lowest sequencing depth (2293). We then evaluated the effects of our treatments on ASV richness using Poisson generalized linear models, correcting the standard errors using a quasi-GLM model, since we detected overdispersion in our data (Cameron and Trivedi 1990; Zuur et al. 2013), and used ANOVA for the Shannon index. Finally, we explored the effect of *S. inaequidens* height and lateral growth on invaded-range bacterial alpha diversity, i.e., ASV richness and the Shannon index, using a linear model.

## Results

By day 84, *S. inaequidens* individuals were still alive in at least three replicates per treatment combination. Specifically, all five replicates survived in the control and in the invaded-range (Italy) community under non-autoclaved soil; four replicates survived in the same treatments under autoclaved soil; and three replicates remained in each of the other treatment combinations.

### Effect of competition and soil biota conditions on *Senecio* performance

*Senecio inaequidens* performance was affected more by the community with which it grew than by soil conditions. The maximum height of *S. inaequidens* plants was significantly reduced when growing in competition with plants from the South

African range compared to the control treatment in pots with no competitor community (ANOVA: Community: $F = 4.31$, $p = 0.03$; Fig. 1; Suppl. material 1: table S3). Soil autoclaving did not have a significant effect on the average height of *S. inaequidens* (ANOVA: Soil: $F = 1.27$, $p = 0.27$). We also did not find an effect of community or soil conditions on lateral growth (ANOVA: Community: $F = 1.04$, $p = 0.37$; Soil: $F = 2.46$, $p = 0.13$; Fig. 1).

## Close phylogenetic relatedness to competitor species modulates *Senecio* performance

Before exploring the effect of relatedness on *S. inaequidens*, we eliminated an outlier from the calculations of weighted phylogenetic distances because its value was above 1.5 times the interquartile range. This value emerged from the dominance of one competitor species and the mortality of all other natives in one community. We then ran models with and without soil as an explanatory variable and compared them. Because soil effects did not improve model fit, we excluded this variable and focused on models based on phylogenetic distance. We did not find a significant effect of community-weighted phylogenetic distances on either maximum height or lateral growth (LM: $R\text{-squared}_{height} = -0.08$, $p = 0.91$, $\text{R-squared}_{lat.\ growth} = -0.08$, $p = 0.88$; Fig. 2; Suppl. material 1: table S4). For the distance of the most abundant competitor species to *S. inaequidens*, we found a significant relationship with the height of *S. inaequidens* (LM: $R$-squared = 0.32, $p = 0.02$; Fig. 2; Suppl. material 1: table S4), although for lateral growth the effect was not significant (R-squared = 0.19, $p = 0.06$). *Wahlenbergia undulata* and *W. androsacea* (SA community) were the most phylogenetically similar species to *S. inaequidens* (Suppl. material 1: fig. S2).

## Correlation between soil bacterial communities and *Senecio* performance

The analysis of soil bacterial communities yielded a total of 687,210 valid sequences, ranging between 2293 and 199,736 per sample, from which 8471 ASVs were inferred. At the phylum level, 46.8 ± 6.1% of sequences were classified as Pseudomonadota, 20.7 ± 7.1% as Actinomycetota, and 10.6 ± 3.1% as Bacteroidota (Suppl. material 1: fig. S3, table S5). At the genus level, 60.0 ± 9.6% of sequences could not be classified. Unclassified bacteria were particularly abundant (9.5 ± 2.7%), as were unclassified members of the classes Beta- and Gammaproteobacteria (5.4 ± 2.8% and 4.8 ± 2.0%, respectively). The most abundant classified genus was *Streptomyces*, with 3.9 ± 3.4% mean abundance (Suppl. material 1: table S6). The NMDS plot showed a clear separation of samples from autoclaved soil in pots where *S. inaequidens* grew alone (CTR; Fig. 3A). Samples from the native-range community (SA) showed greater dispersion, whereas samples from the invaded-range community (IT), regardless of soil condition, clustered more closely (Fig. 3A). Our PERMANOVA test accounted for 47.27% of the overall variation and indicated an effect of both competitor community identity and soil, but not their interaction, on ASV community structure (PERMANOVA: Community $F = 0.23378$, $p = 0.001$; Soil $F = 0.11063$, $p = 0.003$; Suppl. material 1: table S7).

We found that the highest richness and the Shannon diversity of ASVs occurred in non-autoclaved soils from the South African communities and the lowest in autoclaved soil with no competitor species (control). There was a significant inter-

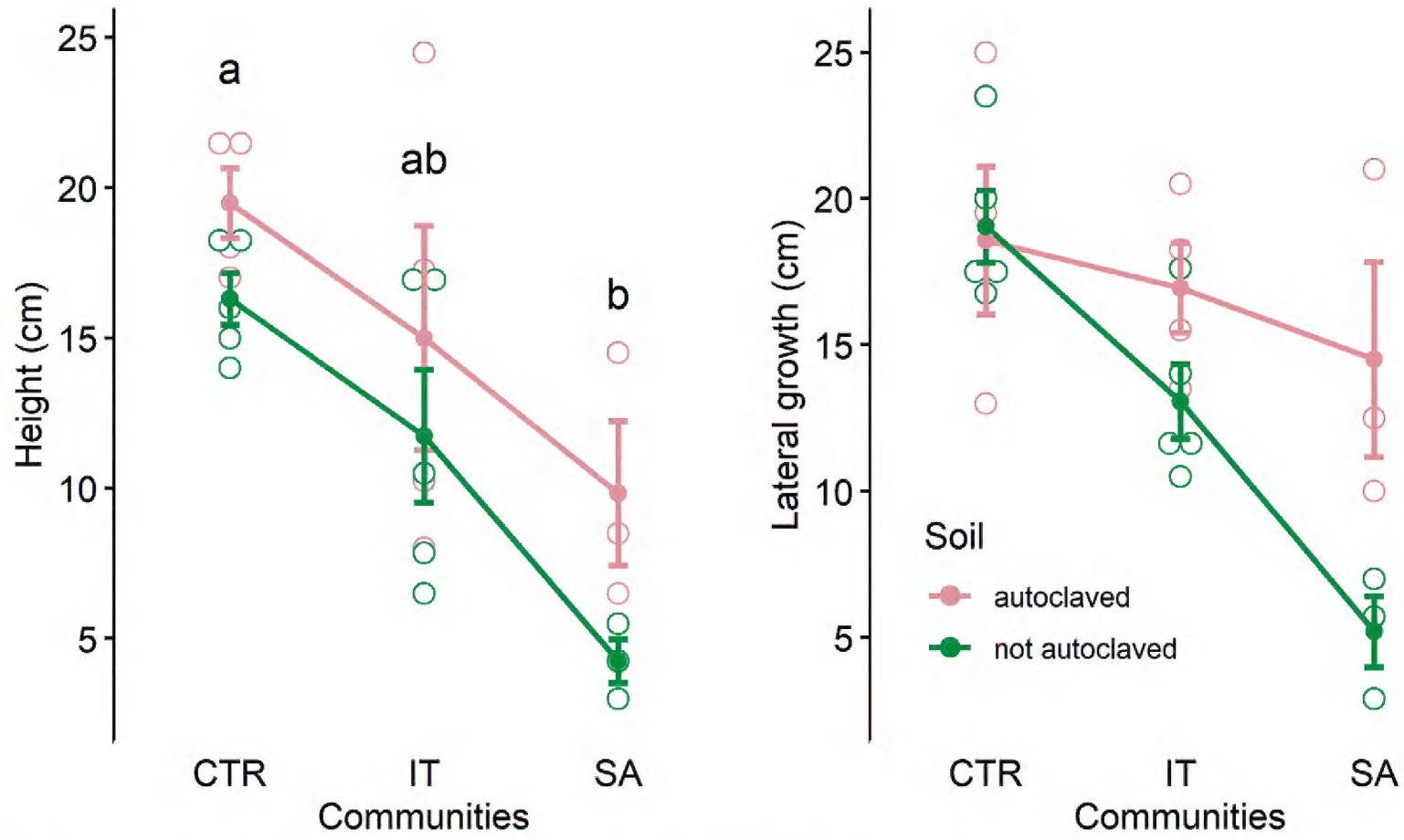


**Figure 1.** Differences among community and soil treatments in height (left panel) and lateral growth (right panel) of *Senecio inaequidens* 84 days after the experiment started. The control treatment (CTR) consists of *S. inaequidens* plants growing alone; IT represents the evolutionarily naïve community from the invaded range in Italy, and SA represents the evolutionarily experienced community from the native range in South Africa (ANOVA: Community: $F = 4.31$, $p = 0.03$). Autoclaved soil is represented in light pink and non-autoclaved soil in green. Different letters indicate significant differences among treatments ($p < 0.05$), and error bars represent standard errors.

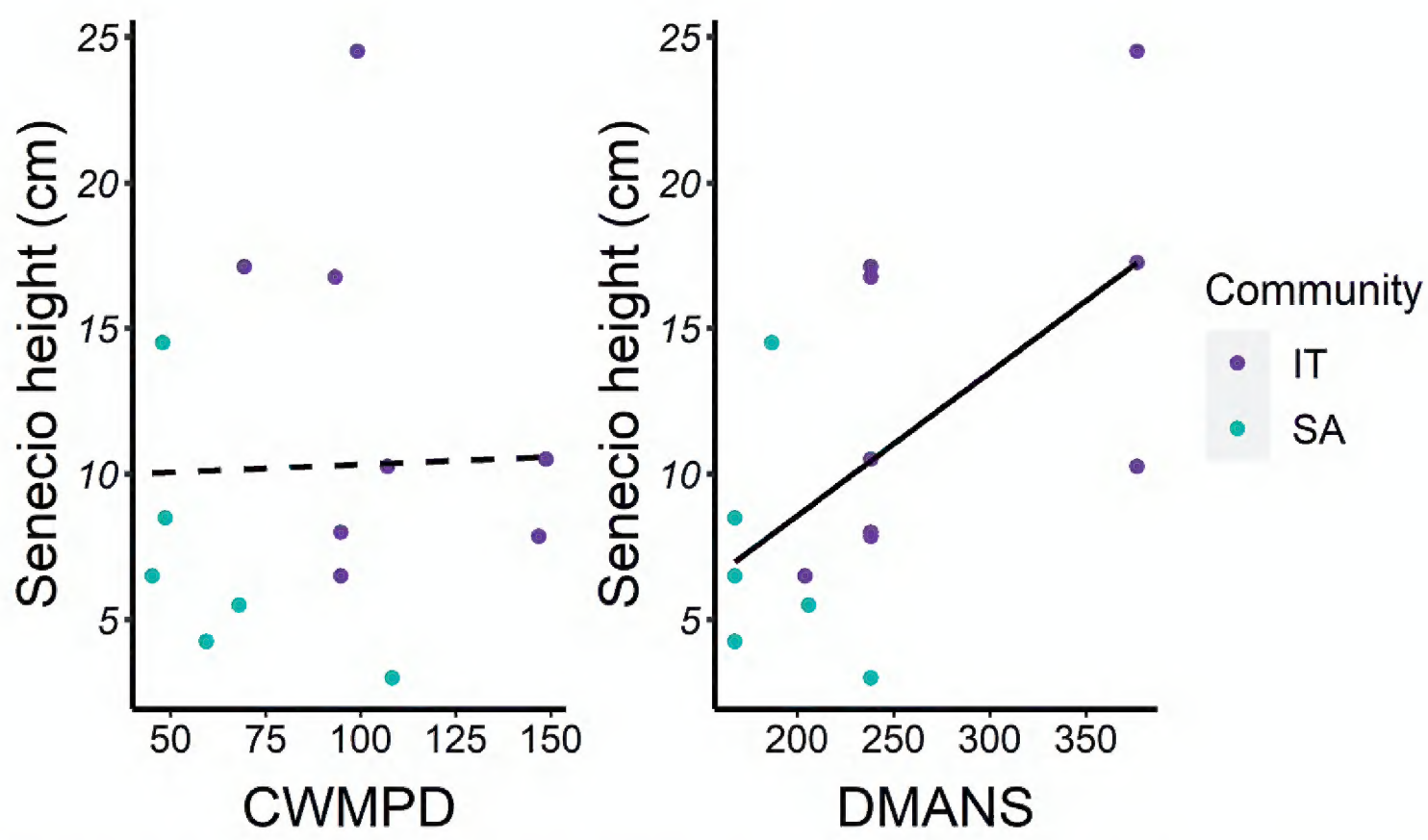


**Figure 2.** Relationship between the height of *Senecio inaequidens* and two measures of phylogenetic distance between *S. inaequidens* and the competitor species: (left panel) community-weighted phylogenetic distances ($R$-squared = –0.07, $p = 0.78$); (right panel) phylogenetic distance of the most abundant species in each community to *S. inaequidens* ($R$-squared = 0.32, $p = 0.02$). IT represents the community from the invaded range in Italy (in purple), and SA represents the community from the native range in South Africa (in turquoise).

action between competitor community identity and soil conditions for bacterial ASVs (GLM, $p < 0.05$; ANOVA, $F = 4.25$, $p = 0.03$; Suppl. material 1: table S8). Specifically, the effect that community had on ASV richness was modified by soil conditions, with lower ASV richness and diversity in controls and South African communities growing in autoclaved soil compared to non-autoclaved conditions.

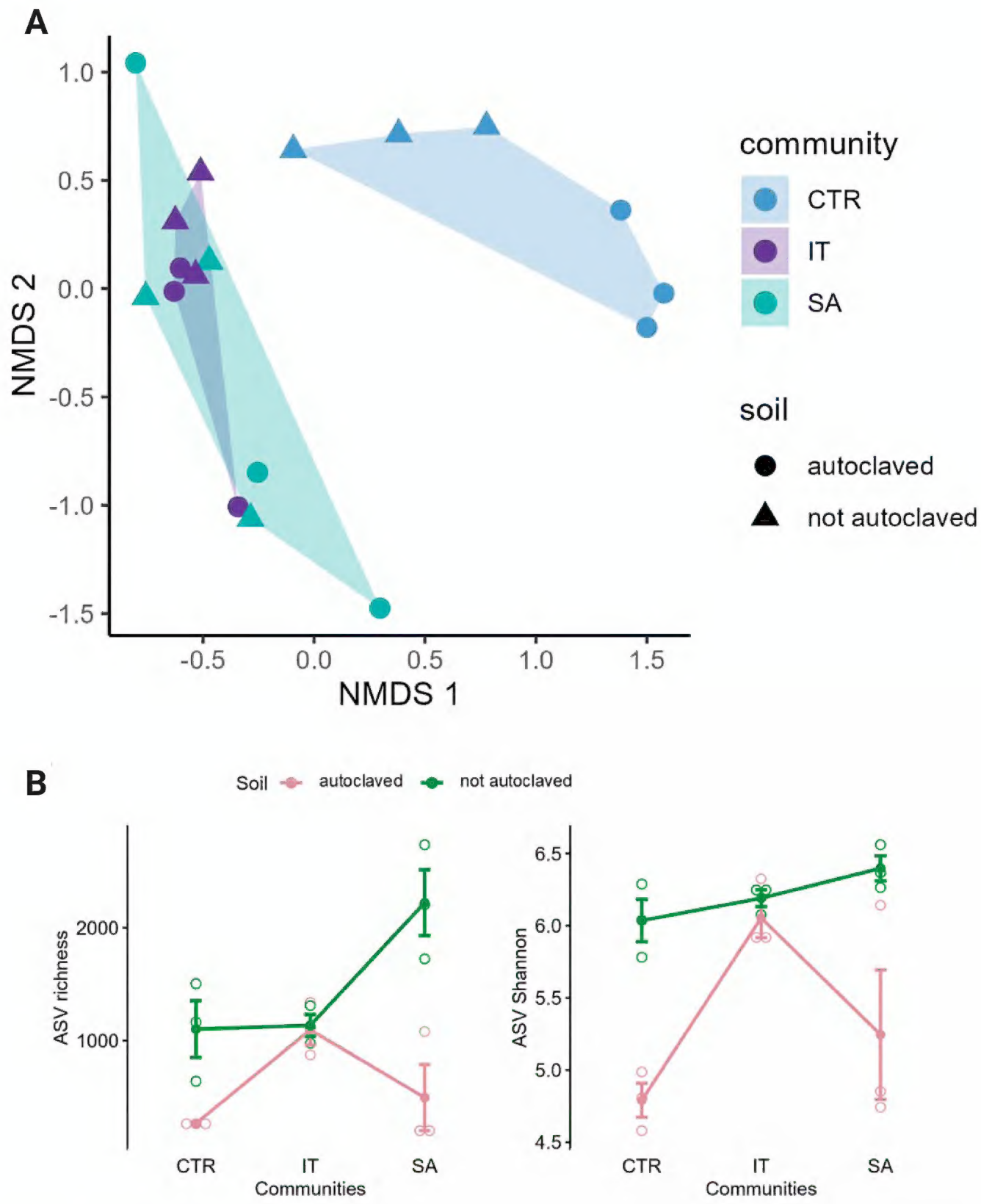


**Figure 3. A.** Two-dimensional plot of the non-metric multidimensional scaling analysis (NMDS) for bacterial ASVs. The control treatment (CTR) is shown in light blue, the community from the invaded range in Italy (IT) in purple, and the native-range community (SA; South Africa) in turquoise. Autoclaved soil treatment is represented with filled circles and non-autoclaved soil with filled triangles; **B.** Differences among community and soil treatments in ASV richness and the Shannon index of soil bacterial communities. Error bars represent standard errors. Autoclaved soil is represented in light pink and non-autoclaved soil in green. ASV richness: interaction, $p < 0.05$; Shannon index (ANOVA: Community $F = 5.699$, $p < 0.05$; Soil $F = 24.082$, $p < 0.001$; Interaction $F = 4.254$, $p = 0.04$).

Furthermore, ASV richness and diversity in Italian communities did not differ between soil conditions (Fig. 3B).

Height and lateral growth of *S. inaequidens* had a statistically significant negative relationship with both ASV richness and the Shannon index, with taller and wider individuals associated with lower soil bacterial diversity (LM ASV richness: Adj-$R^2$(height) = 0.32, $p = 0.01$, Adj-$R^2$(lateral growth) = 0.18, $p = 0.04$, LM ASV Shannon: Adj-$R^2$(height) = 0.39, $p = 0.003$, Adj-$R^2$(lateral growth) = 0.14, $p = 0.067$; Fig. 4; Suppl. material 1: table S9).

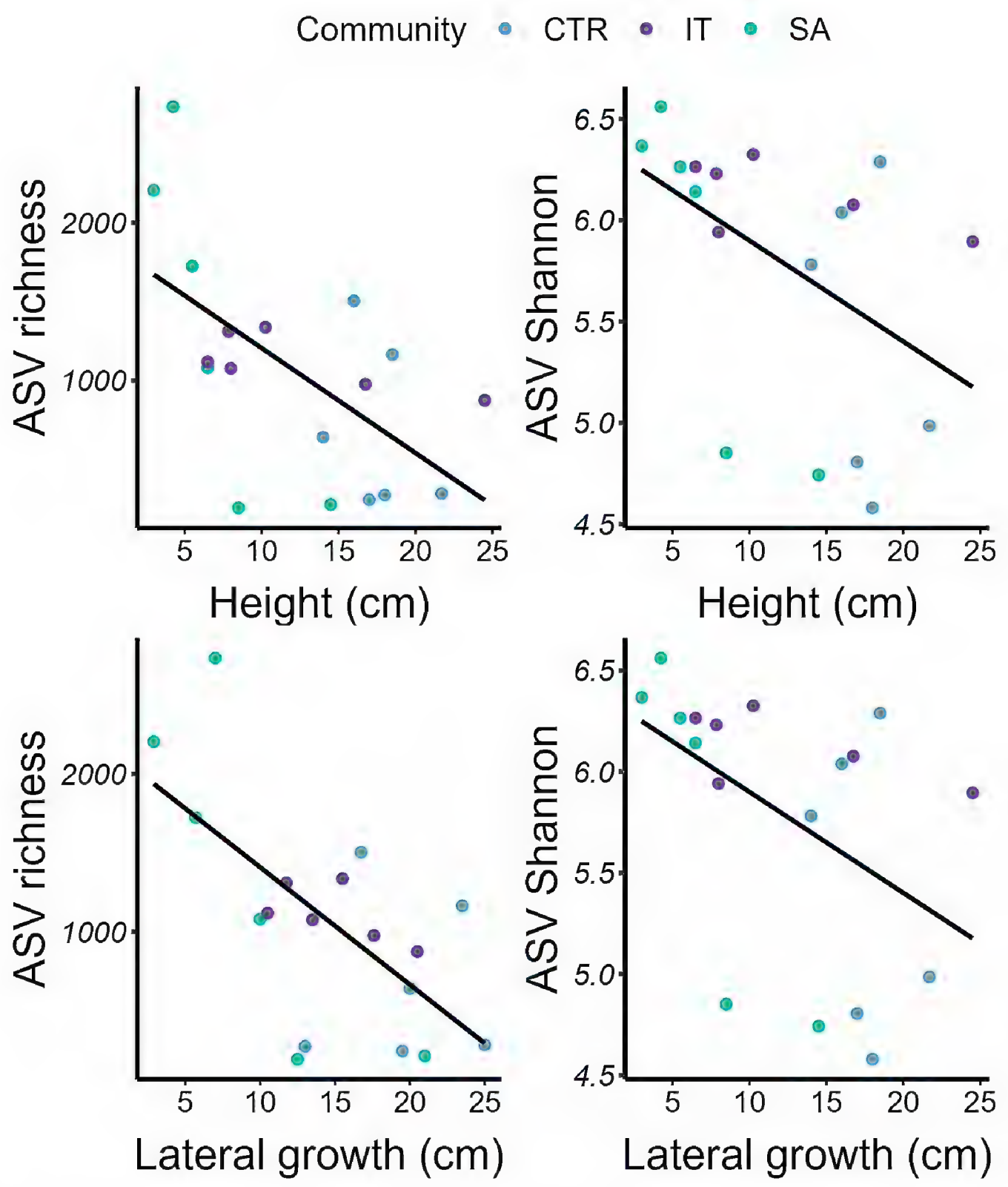


**Figure 4.** Linear model results for the relationship between height and lateral growth of *Senecio inaequidens* and soil bacterial diversity, represented as ASV richness and Shannon index (LM ASV richness: Adj-$R^2$(height) = 0.32, $p$ = 0.01, Adj-$R^2$(lateral growth) = 0.18, $p$ = 0.04, LM ASV Shannon: Adj-$R^2$(height) = 0.39, $p$ = 0.003, Adj-$R^2$(lateral growth) = 0.14, $p$ = 0.067). For reference, the identity of the competing communities is indicated in different colors.

## Discussion

With our experiment, we investigated how the eco-evolutionary experience of species in the resident community and the soil biotic conditions influence *Senecio inaequidens* invasion success. As hypothesized, the identity of competing plant communities significantly affected *S. inaequidens* growth, supporting the hypothesis that competition with species from the invaded range seems to be less intense than with plant species from the native range. The effect of increased phylogenetic distance in explaining *S. inaequidens* performance was mixed, with no effect of community-wide distances but a significant influence of the phylogenetic distance of *S. inaequidens* to the most abundant species in the community. Although their competitive responses to the plant communities were not significantly affected by autoclaving the soil in which they grew, we found large *Senecio* plants to be associated with low bacterial diversity in the sampled pots.

## Eco-evolutionary naivety and divergence shape invasion success

Our results align with previous studies indicating that naïve species in the invaded range may lack evolved resistance or competitive strategies against introduced species with which they have had no similar interactions in their evolutionary history (Callaway et al. 2011; Saul et al. 2013; Zheng et al. 2018). For instance, in a removal experiment, Callaway et al. (2011) found *Centaurea stoebe* L. populations in their native range (Europe) to exhibit a significantly higher response (6.5- to 7.5-fold) to the removal of neighboring plants compared to populations in their invaded range (North America). The stronger competitive response observed for *S. inaequidens* when growing in competition with Italian communities may therefore stem from their limited eco-evolutionary experience with the target alien. This could be explained by several mechanisms, including differences in resource acquisition strategies that limit *Senecio* suppression or a subtle temporal advantage, allowing *S. inaequidens* to grow slightly faster and establish early dominance. Indeed, Delory et al. (2019) found *S. inaequidens* to exhibit strong competitive effects on native plants when it has a temporal advantage due to, for example, the slower growth of competitor species. Another potential explanation is the release of allelopathic chemicals by *Senecio*, which may affect plants in the invaded range that are not yet adapted to them (Weißhuhn and Prati 2009). While our experiment was not designed to disentangle these mechanisms, future work should aim to test their relative contributions to invasion success. We also acknowledge that seeds from species in the invaded range were collected from areas where *S. inaequidens* was already present, so they may have already undergone some degree of adaptive exposure to the invader.

The two phylogenetic metrics produced different numerical ranges because they captured distinct aspects of community structure, consistent with previous studies (e.g., Yannelli et al. 2017). The community-weighted phylogenetic distance, which resulted in broader phylogenetic scales by integrating both common and rare species, showed no relationship with the performance of *S. inaequidens*. In contrast, increased relatedness to dominant competitors, characterized by smaller phylogenetic distances (e.g., *Wahlenbergia* sp.), was associated with reduced *S. inaequidens* growth. This pattern suggests that dominant species exert stronger competitive effects than the community as a whole, supporting Darwin's naturalization hypothesis (Yannelli et al. 2025) and the idea that close phylogenetic relatedness indicates greater overlap in resource use and, consequently, more intense competition (Divíšek et al. 2018). Our results also align with previous research showing that phylogenetic similarity to dominant plant species predicts biotic resistance to invasive herbaceous plants, such as *Ambrosia artemisiifolia* L. and *Solidago gigantea* Aiton (Yannelli et al. 2017), in assembled communities. Taken together, these results indicate that interactions with key species within the community, particularly the most abundant ones, may play a critical role in biotic resistance to invasion.

In contrast to our findings, an observational study in Northern Italy found that *S. inaequidens* performed better in communities with high phylogenetic relatedness, based on community-weighted phylogenetic distance (Quaglini et al. 2025a), especially in more productive habitats. These results supported the pre-adaptation hypothesis, which states that introduced species that are phylogenetically more similar to the natives are more likely to establish successfully, as they may share similar environmental adaptations (Darwin 1859). Such apparently contradictory outcomes could be reconciled by recent reviews suggesting that Darwin's natural-

ization and pre-adaptation hypotheses are not mutually exclusive but may operate at different spatial scales (Thuiller et al. 2010; Ma et al. 2016). Namely, successful alien species would be more closely related to natives at broader spatial scales due to environmental filtering but more distantly related at finer spatial scales, where competition for limiting resources becomes more important (Ma et al. 2016). This highlights the context dependence of biotic resistance, where competition dynamics can shift depending on scale, environmental conditions, and resource levels.

## Linkages between soil bacterial communities and *Senecio* performance

We observed distinct proportions of the most abundant bacterial phyla across treatments, mainly Pseudomonadota and Actinomycetota. Soils with South African competing plant species exhibited slightly higher levels of Actinomycetota, whereas those with Italian species had more Pseudomonadota. Both phyla are highly diverse, widespread, and common across various habitats in Europe (van Bergeijk et al. 2020; Labouyrie et al. 2023). The composition of the plant communities in the pots was strongly associated with differences in soil bacterial assemblages and diversity. At the time of sampling, soils from the two competing communities were more similar to each other than to the controls, with those containing South African plants having the most diverse soil bacterial community structures. In contrast, control pots with *S. inaequidens* individuals growing alone harbored distinct communities, with no overlap in bacterial community structures. For instance, autoclaved soils in control pots showed the lowest bacterial richness and diversity and were characterized by a higher relative abundance of *Nocardioides* (10.0% on average) compared to other treatments. Except for soils in treatments with plants from the Italian range, autoclaving generally reduced bacterial richness and diversity, indicating a lasting effect of sterilization. Soils from pots with Italian species maintained relatively similar community structures and diversity across soil treatments. Overall, these patterns suggest that plant community identity is closely correlated with microbial community assembly, even after sterilization. One possible explanation is that plants introduce or promote specific bacterial taxa associated with their seeds or rhizospheres (Gundale et al. 2016).

Taller and wider *Senecio inaequidens* individuals tended to be associated with soils with lower bacterial richness and diversity, suggesting that *Senecio* performance correlated with bacterial community patterns. This association aligns with previous findings showing that *S. inaequidens* traits, particularly those related to competitive ability and resource allocation, are correlated with variation in rhizosphere bacterial diversity (e.g., Thébault et al. 2010). Although we cannot infer causality, one possible explanation is that allelopathic compounds produced by *S. inaequidens*, such as pyrrolizidine alkaloids, may influence microbial assemblages (Joosten and van Veen 2011). Interestingly, soils in South African species treatments, where *S. inaequidens* performed poorly, supported the most diverse bacterial communities. This pattern could reflect interactions with co-introduced or generalist soil pathogens associated with native-range species (Li and Shao 2024), potentially enhancing their competitive effects. This may have been reflected in *S. inaequidens*' slightly higher growth in autoclaved compared to non-autoclaved soils within South African treatments, although this difference was not statistically significant ($p = 0.5$).

It is important to note that methods such as autoclaving can alter soil chemistry, nutrient availability, and physical structure, potentially confounding experimental

results by affecting both microbial communities and abiotic factors (Perkins et al. 2013). However, since samples for bacterial analysis were collected after plants had been growing in these soils, residual DNA from cells killed approximately 90 days earlier is probably negligible. Finally, the 84-day duration of the experiment provided valuable insights, although longer-term studies could offer a more comprehensive understanding of plant–soil feedbacks and competitive dynamics (Liu et al. 2024).

## Conclusion and implications for management

Our study highlights the interplay between eco-evolutionary experience, plant phylogenetic relationships, and soil biotic conditions. By analyzing the interactions between this invasive species and plant communities from both its native and invaded ranges, we provide insights into the possible mechanisms driving its invasion success, which seems to be favored by the inexperience of the community in the invaded range with respect to the invader (i.e., naivety). Based on our findings, we argue that selecting a few phylogenetically related species at high abundances to outcompete *S. inaequidens* could be a promising practice for management in areas under restoration. In particular, the observation that *S. inaequidens* performs better in the presence of naïve species and lower microbial diversity indicates that restoration efforts might benefit from enhancing the competitive ability of native species and promoting microbial diversity. This could involve the selection of native species that are closely related to the invader or have strong competitive abilities and testing soil amendments to increase microbial diversity and resilience. Furthermore, our findings suggest that management strategies should also consider the composition and functional roles of native communities by selecting multi-species suites of closely related competitors displaying similar trait profiles, as well as the structure of soil microbial communities.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

### Use of AI

We used OpenAI's ChatGPT to assist with language refinement in several sentences and to generate an illustrative figure of the experimental design. All content was reviewed and edited by the authors.

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## Author contributions

LAQ: Conceptualization, Formal analysis, Methodology, Writing – original draft, Investigation; FAY: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft, Supervision, Project administration; IG: Methodology, Software, Formal analysis, Visualization, Data curation, Writing – review and editing; AF: Methodology, Writing – review and editing; SC: Methodology, Writing – review and editing; CM: Resources, Methodology, Writing – review and editing; CC: Resources, Methodology, Writing – review and editing; JMJ: Conceptualization, Writing – review and editing; SC: Project administration, Writing – review and editing; RG: Conceptualization, Supervision, Project administration, Funding acquisition. All authors have read and agreed to the published version of the manuscript.

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## Data availability

The data generated in this study are freely available in the Zenodo Repository via https://doi.org/10.5281/zenodo.18503161.

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## Supplementary material 1

**Supplementary information with descriptions, figures and tables**

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